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THE MODE OF GROWTH OF THE RADIATES.

BY A. S. PACKARD, JR.

I. THE HYDROIDA.

THE animal next higher in structure than the sponge is the curious Protohydra discovered by Greef among diatoms and seaweeds in the oyster park at Ostend. It is regarded by Greef as the marine ancestral form of the Cœlenterates (Hydroids, Jelly fishes and Actiniæ). It is the simplest possible radiate form yet discovered. As the form of the fresh-water Hydra is familiar, Protohydra may be best described as similar to that, except that it is entirely wanting in tentacles. Like Hydra it is made up of two layers (an ectoderm and endoderm), with a mouth and stomach (gastro-vascular cavity). Nothing is known of its history, though Greef is positive that it is not a young Actinia.

The next highest form is the fresh-water Hydra, which is commonly found on the under side of the leaves of aquatic plants. This well known animal is the simplest form of the division of radiates known as Hydroids. The somewhat club-shaped body consists of two layers, the inner (endoderm) lining the general cavity of the body, which serves both as mouth and stomach and for the circulation of the nutritive fluid, and is called the gastro-vascular cavity. The mouth is surrounded with eight tentacles, which are prolongations of the body-wall and are hollow, communicating with the body cavity.

Such is the general structure of the Hydra. In the ectoderm are situated the lasso-cells or nettling organs, being minute barbed filaments coiled up in a cell-wall. From Kleinenberg's recent researches on the Hydra it appears that there are scattered irregularly through the endodermal lining of the body-cavity isolated ciliated cells. They do not form a continuous lining membrane, and thus bear an interesting analogy to the ciliated cells of the sponge. While the endoderm forms a simple cell-layer, the outer layer (ectoderm) is more complex, as just within an external simple layer of large cells is a multitude of smaller cells, some of them being thread or lasso cells, while still within are fine muscular fibrillæ which form a continuous layer. The large cells first named end in fibre-like processes, which alone possess contractility and are thought by Kleinenberg to be motor-nerve endings. These large cells, from combining the functions of muscle and nerve, are termed "nervo-muscle cells." The little cavities between the large endodermal cells and the muscular layer which lies next to the endoderm is filled with small cells and lasso-cells, forming what Kleinenberg calls the interstitial tissue. From this tissue are developed the eggs and spermatozoa.

The organization of all the hydroids and even Lucernaria and the larger jelly-fishes (Discophora) is based on the plan of the Hydra. They all have a simple body-cavity, but no true alimentary canal surrounded by a perivisceral cavity. This is the distinguishing character of the Cœlenterates. In the jelly-fishes, the often complicated water vascular system of canals are simply passages leading out from the axial gastro-vascular cavity. If we place a jelly fish in the same position as the Hydra, *i.e.*, with the tentacles directed upwards, the general homology between the parts can be clearly traced. In the Hydroids, such as Sertularia, etc., the ectoderm is surrounded by a chitinous sheath, secreted from this layer. While in Hydra the young bud out from the side of the body, in the Hydroids the young are developed on a separate stalk from the barren or nutritive stalk or "zooid." The individual Hydroid is thus subdivided into a reproductive and a nutritive zooid. The reproductive zooids seldom or never take in food, but are nourished by the nutritive zooids, the two zooids being connected by a common creeping stem called the "cœnosarc."

The Anthozoa or sea anemones and coral polypes differ from the Hydroids and Medusæ in having the stomach open at the bottom into a second and larger cavity communicating with the radiating chambers. In the Ctenophora there is a decided approach in the complication of the body to the Echinoderms. The radiated structure so clearly shown in the lower forms is here in part subordinated to the bilateral arrangement of parts; they have a right side and a left side. They also differ in the mouth opening into a wide digestive cavity, enclosed between two vertical tubes, uniting at the end of the body, where the stomach forms a reservoir for the gastro-vascular tubes ramifying throughout the body. They move by a peculiar apparatus consisting of bands of comb-like flappers. Not detaining the reader with a definition of the subdivisions of the Cœlenterates we shall be content with giving the following tabular view of the lowest subdivision of Radiates :—

CŒLENTERATA.

- ACALEPHS OR HYDROZOA.
  - 1. *Hydroida.* *a.* Hydriform (Hydra, Hydractinia, Tubularia, Sertularia)
    - *b.* Siphonophora (Velella, Agalma, Physalia).
  - 2. *Calycozoa* (Lucernaria).
  - 3. *Medusæ* or *Discophoræ* (Aurelia.)
- ANTHOZOA (Actinia, Cerianthus, Astræa, Alcyonium, Gorgonia and Renilla).
- CTENOPHORÆ (Beroë, Cydippe, Cestum).

Development of Hydra and the Hydroids. Ehrenberg first showed that the Hydra reproduced by eggs which become fertilized by spermatic particles. Kleinenberg describes the testis, which is lodged in the ectoderm and which develops tailed spermatozoa like those of the higher animals. They arise, as in other higher animals, from a self-division of the nuclei of the testis-cells. There is a true ovary formed in the same interstitial tissue of the ectoderm, consisting of a group of cells, which differ entirely in their mode of formation from the ovaries (gonophores) of the marine Hydroids, which are genuine buds.

It thus seems that Hydra is monœcious or hermaphrodite, *i. e.*, the sexes are not distinct. The egg of Hydra originates from the central cell of the ovary; thus confirming the opinion now generally held that all animals as a rule arise from a simple cell. After the egg-cell has escaped from the ovary through the ectoderm, it still holds on by a narrow point to the sides of the Hydra, where it is fecundated by the spermatic particles discharged into the surrounding water from the testis.

Fecundation is succeeded by a true segmentation of the egg. The young Hydra thus passes through a true "Morula" stage.[1] There is an outer layer of prismatic cells, forming the surface of the germs, and surrounding the inner mass of polygonal cells. At first none of these cells are nucleated, but afterwards nuclei appear, and it is an important fact that these nuclei do not arise from any preëxistent egg-nucleus.

The next step is the formation of a true chitinous shell, enveloping the germ or embryo. After this Kleinenberg asserts that the cells of the germ become fused together, and that the germ is like an unsegmented egg, being a single continuous mass of protoplasm. Allman remarks that "as this phenomenon does not occur in other Hydroids it can have no general significance for the development of the order."

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[1] Hereafter we shall often use Hæckel's convenient term "Morula;" instead of "stage of segmentation of the egg," for the sake of brevity.

The remaining history of Hydra is soon told. In this protoplasmic germ-mass there is formed a small excentric cavity; this is the beginning of the body-cavity, which finally forms a closed sac. Allman remarks on this discovery of Kleinenberg's that "it is clear that the formation of a body cavity by invagination of the walls [*i. e.*, ectoderm] with the significance which Kowalevsky has assigned to it in other animals, does not exist in Hydra, and just as little will it be found in any other hydroid." It will be seen farther on that in certain medusæ, Kowalevsky has discovered that the digestive cavity is formed by the invagination of the ectoderm, and we have seen (p. 107) that Metznikoff declares that the ciliated cells lining the gastro-vascular cavity in the embryo of the sponge are the originally external ciliated cells of the planula withdrawn into and lining the body cavity.

After several weeks the germ bursts the hard shell and escapes into the surrounding water, but is still surrounded by a thin inner shell. After this a clear superficial zone appears, and a darker one beneath, which is the first indication of the splitting of the germ into the two definitive germ-lamellæ, common to all animals except the one-celled Protozoa.

The embryo soon stretches itself out, a star-shaped cleft appears, which forms the mouth. The tentacles next appear. The animal now bursts open the thin inner shell, and the young Hydra appears much like its parent form.

There is, then, no metamorphosis in the Hydra; no ciliated planula. The adult form is thus reached by a continuous growth.

It will be seen, to anticipate somewhat, that the Hydra, exactly as in the vertebrates, including man, arises from an egg developed from a true ovary, which is fertilized by a true tailed spermatic particle; that the egg passes through a morula stage; that the germ consists of two germinal layers, while from the outer layer, as probably in the vertebrates, an intermediate or nervo-muscular layer is formed, which Allman thinks is the homologue of the middle germ-lamella of the vertebrates, supposed to have originally split off from the ectoderm. Allman even regards the chitinous shell of the germ of Hydra as the equivalent of the epidermis of vertebrates, being a provisional embryonic organ in Hydra, but permanent in vertebrates.

In all the marine Hydroïds, which are more complex in their individualism than Hydra, the sexes being separate, the eggs and spermatic particles are thought by Allman to be developed from the endoderm. But E. Van Beneden has on the other hand shown that the eggs in Hydractinia are exclusively developed from the endoderm, while the spermatic cells arise from the ectoderm.

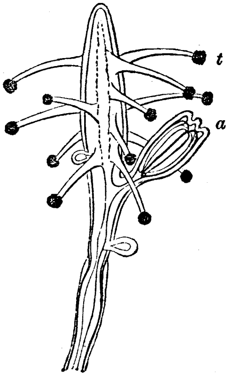
The simplest form next to Hydra is Hydractinia, in which the individual is differentiated into three sets of zooids; *i.e.*, *a*, hydra-like, sterile or nutritive zooids; *b* and *c*, the reproductive zooids, one male and the other female, both being much alike externally, having below the short rudimentary tentacles several spherical sacs, which produce either male or female medusæ. These medusa buds or closed generative sacs are fundamentally like the free medusæ in structure. The marine Hydroids, then, are universally diœcious, and usually each colony is either male or female.

A rather more complicated form is the common *Coryne mirabilis.* Fig. 51 shows the hydrarium with its long tentacles (*t*) and *a* the medusa buds, Fig. 52 its free medusa. Tubularia is a higher form, and allied to the latter is still another form, *Corymorpha pendula* (Fig. 53. After Agassiz).

Figs. 54–58 (after A. Agassiz) represent quite fully the life history of another Tubularian, *Bougainvillia superciliaris.* Fig. 54 represents the hydrarium, with the sterile zooids provided with long tentacles, and the medusa buds of different ages. Fig. 55 shows a bud still more enlarged, with the proboscis (manubrium) just formed, and knob-like, rudimentary tentacles. In an older stage (Fig. 56) the proboscis is enlarged and the tentacles lengthened, while the depression at the upper end indicates the future opening. In Fig. 57 the appendages of the proboscis are plainly indicated, the tentacles are turned outwards. Shortly after this the jelly-fish breaks loose from its attachment and swims around as at Fig. 58.

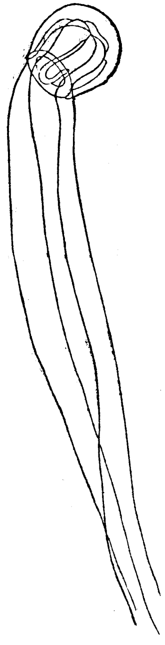
How do the zooids first arise? This leads us to speak of the simplest mode of reproduction in the Hydroids, which is by budding. The object of sexual reproduction, *i. e.*, by eggs and spermatozoa, throughout the animal and plant world, is by bringing the germ or portion of protoplasm of one individual, which is an epitome potentially of its physical and psychical nature, to mingle with that of another of the same species, so that the offspring may combine the qualities of both parents, and not deteriorate. The species can be reproduced simply by budding, but the result would, if maintained for a number of generations, in the end prove disastrous to its integrity. Nature abhors self-fertilization. So that while, as in these Hydroids, the zooid form may be produced by budding, yet the time comes when the individuals of one colony must mingle their reproductive elements with those of a remote colony, through the medium of the water. By this mode of reproduction new colonies are also set up. On the other hand budding or gemmation has for its object the extension of the colony of nutritive and reproductive zooids. This alternation of budding with sexual generation or "alternation of generations," or "parthenogenesis," is first met with in the Hydroids, and we shall find it often recurring in the higher animals when needed to meet some special exigency of the species.

Fig. 51.



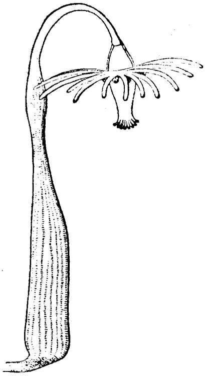
Polypite of Coryne mirabilis, with a bud below *a*, and medusa bud, (gonophore) above, *a*, much enlarged. After Agassiz.

Fig. 52.



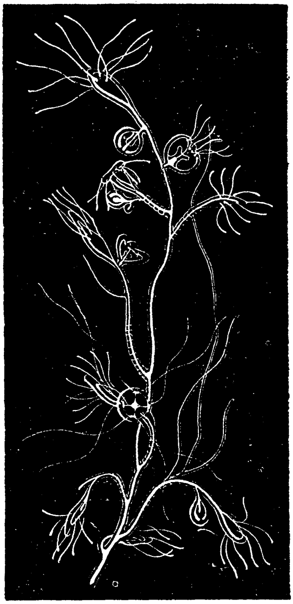
Free medusa of Coryne thrown off from the gonophore. Natural size. After Agassiz.

Fig. 53.



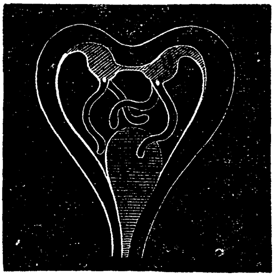
Corymorpha.

Fig 54.



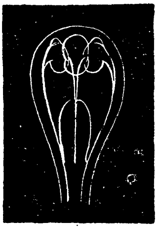
Hydrarium of Bougainvillia, magnified.

Fig. 56.



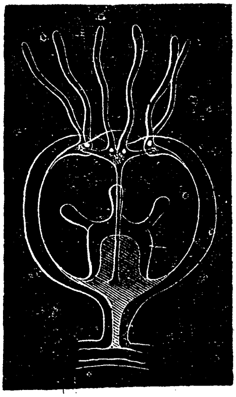
Medusa bud of 54, farther advanced.

Fig. 55.



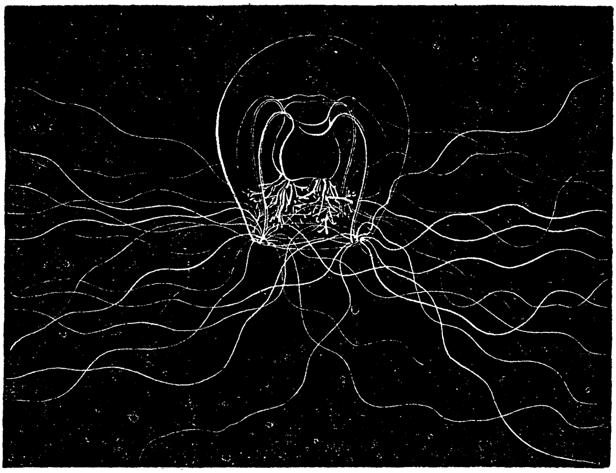
Medusa bud of 54.

Fig. 57.



Medusa bud with the tentacles turned out. Magnified.

Fig. 58.



Medusa of Bougainvillia. Magnified. After A. Agassiz.

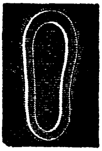
Budding begins as a slight protrusion of the basal portion (cœnosarc) of the colony, which then becomes spherical and finally club-shaped, as in Fig. 51, until it assumes the form of a zooid. It remains permanently attached in all the Hydroids except in Hydra, where it breaks off and bears a free individual. In some species of Tubularia the heads of the zooids successively drop off, and are renewed.

Multiplication by fission has only been observed in one case, in the medusa of Stomobrachium, observed by Kölliker at Messina. In this the pendent stomach divided in two, becoming doubled, which was followed by a vertical division of the umbrella, separating the animal into two independent halves. These again subdivided, and Kölliker thinks this process went on still farther.

The second mode of generation, *i. e.*, by eggs and spermatic particles, have been observed in many marine Hydroids. As in the Hydra, the eggs, after being fertilized, pass through a morula stage, and finally the germ becomes surrounded by a blastoderm, as in Hydra, formed of long prismatic cells directly comparable with the zone of blastodermic cells of insects, and many other animals, including the mammals. The germ elongates and finally escapes from the ovisac (gonophore) of the parent as a ciliated "planula," a term first applied to it by Dalyell.

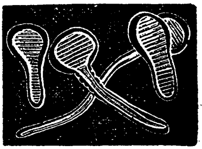
Now how do these planulas become converted into hydras, and through them into medusæ? A glance at the accompanying figures will give the main points in the life history of a not uncommon Hydroid found on our shores, a Melicertum allied to Campanularia (Fig. 62). We are indebted to Mr. A. Agassiz (Seaside Studies in Natural History) for the following facts and illustrations regarding its history. After keeping a number of the Melicertum in a large glass jar for a couple of days at the time of spawning, he found that the ovaries, at first filled with eggs, became emptied, and that the planulæ, at first spherical and afterwards pear-shaped (Fig. 59) swam near the bottom of the jar, and soon attached themselves by the larger end to the bottom of the jar (Fig. 60). "Thus their Hydroid life begins; they elongate gradually, the horny sheath is formed around them, tentacles arise on the upper end, short and stunted at first, but tapering rapidly out into fine, flexible feelers; the stem branches, and we have a little Hydroid community (Fig. 61), upon which, in the course of the following spring, the reproductive calycles containing the medusæ buds will be developed."

Fig. 59.



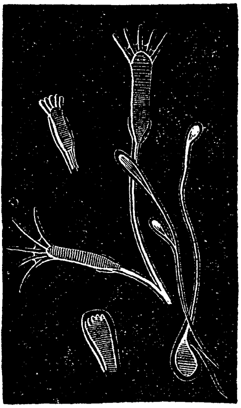
Planula of Melicertum.

Fig. 60.



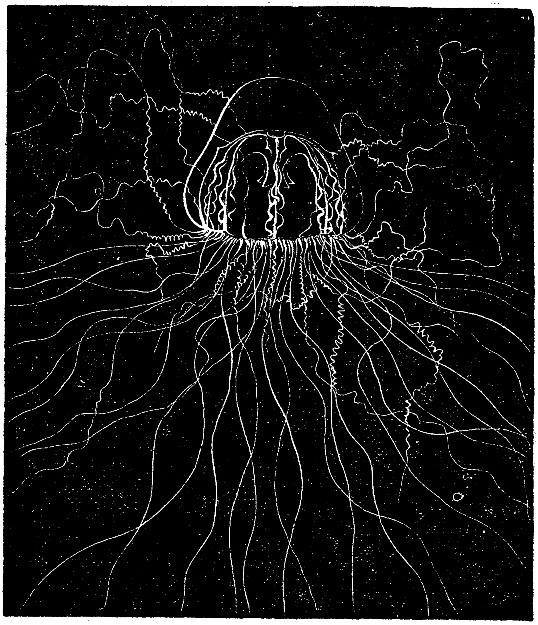
Cluster of Planulæ just attached to the ground.

Fig. 61.



Polypites of Melicertum developed from the planulæ; greatly magnified.

Fig. 62.



Melicertum campanula, seen in profile. Natural size. After Agassiz.

Coming now to the Portuguese man-of-war (Physalia) which have so much occupied the attention of the best naturalists, it would seem at first well nigh impossible to trace their relationship with the ordinary Hydroids. A Physalia may, however, be compared to a fixed colony of Hydractinia or Coryne, for example. Each Physalia is either male or female, and consists of four kinds of zooids; viz., nutritive and reproductive, with medusa buds, which, by their contractions and dilatations propel the colony onward; and the "feeders," a set of digestive tubes which nourish the entire colony.

The Siphonophores (as observed by Gegenbaur, Kowalevsky, Hæckel and Metschnikoff, in Agalma and several other genera) arise from eggs which pass through a morula stage, into a ciliated planula, whose body consists of an ectoderm and endoderm. The gastro-vascular cavity in the Siphonophores, as in the lower Hydroids so far as observed, is formed by a fold of the endoderm, while, as we shall see farther on, in the Discophorous jelly fishes it is formed by an infolding of the ectoderm.

The further development of Nanomia, a Siphonophore native to our northern shores, from the larval state, has been described and figured by Mr. A. Agassiz. To use nearly his own words, the Nanomia consists, when first formed, of an oblong oil bubble, with but one organ, a simple digestive cavity. Soon between the oil bubble and the cavity arise a number of medusa buds, though without any "proboscis" (manubrium), as these medusa buds, called "swimming bells," are destined to "serve the purpose of locomotion only, having no share in the function of feeding the community." After these swimming buds, three kinds of Hydra-like zooids arise. In one set the Hydra is open-mouthed, and is in fact a digestive tube, its gastro-vascular cavity connects with that of the stem, and thus the food taken in is circulated throughout the community. These are the so-called "feeders." The second set of Hydras differ only from the "feeders" in having shorter tentacles twisted like a corkscrew. In the third and last set of Hydras the mouth is closed, and they differ from the others in having a single tentacle instead of a cluster. Their function has not yet been clearly explained. Gradually new individuals are added, until a long chain of Hydroids is formed, which move gracefully through the water, with the oil globule uppermost, which serves as a float and is identical with the large-crested "float" of the Physalia.

Finally, the higher Hydroids, such as Æginopsis, Ægineta Cunina and Lyriope have been found by Muller, Agassiz, McCrady, Leuckart, Gegenbaur, Fritz Muller and others, to develop directly from eggs and pass through a metamorphosis as medusæ. During the past year (1874) Metschnikoff has published, with many figures, an account of the development of Geryonia, Polyxenia (Ægineta) and Æginopsis.

In these animals the egg passes through a morula stage; an outer layer of cells (blastoderm) splits off from the morula, forming the ectoderm and entoderm. The embryo, then, as in Polyxenia, passes through a ciliated planula stage. The embryo may remain spherical, as in Geryonia, or as in Polyxenia and Æginopsis, the body of the planula becomes greatly elongated and bomerang-shaped, and from each end are developed the first two tentacles, then others, and after a slight metamorphosis the adult form is attained.

The life history of the Hydroids comprises, then, the following phases in development:—

1, *a*. Origin of young Hydra by budding.
   b. Origin of embryo from egg fertilized by spermatozoa.
2. Morula stage.
3. Planula (Gastrula) stage.
4. Hydra-like form, attached.
5. Medusa, free and discharging eggs.

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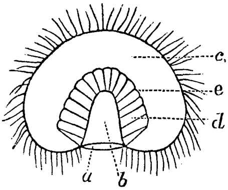
II. THE MEDUSÆ (Discophoræ).

Passing by the Lucernaria, beautiful and interesting, but of whose early development we know nothing, we come to the common larger jelly-fishes of our shores, which differ from the bell-shaped hydroid medusæ in their usually larger size and solid disk, as well as in the larger number and greater complication of the water tubes, which ramify and interbranch along the under side of the disk; and in carrying their eggs in pouches. In our common *Aurelia flavidula* there are four of these large pouches occupying the centre of the disk.

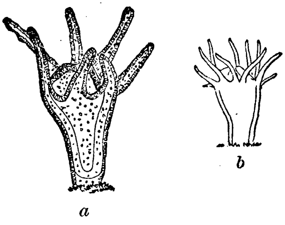
Fig. 63.



Gastrula of an Aurelia-like Medusa.

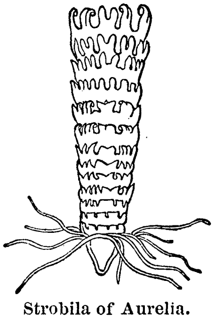
The life history of the Aurelia, which we will select as an example of the mode of development of this group, since it is best known, is far less complicated than that of the Hydroids. The ciliated planulæ may be found in the egg pouches of the female Aurelia during the last of summer. Soon after the ectoderm and entoderm are formed, a mouth is developed, and a gastro-vascular cavity is formed by the invagination of the ectoderm, as stated by Metschnikoff, and they then pass into a gastrula (planula) stage (Fig. 63, Gastrula of a form allied to Aurelia ; *a*, mouth ; *b*, gastro-vascular cavity ; *c*, ectoderm ; *d*, entoderm ; after Metschnikoff), with a mouth and long digestive cavity. After swimming about for a while they fix themselves to some object at the bottom of the sea and soon a pair of tentacles begin to develop, and then two more, until not more than sixteen are developed. When of this hydra-like form (Fig. 64 *a*, young ; *b*, older, after A. Agassiz) it is called a "Scyphistoma," having originally, as well as the Strobila and Ephyra,

Fig. 64.



Scyphistoma of Aurelia, at different ages. Magnified.

Fig. 65.

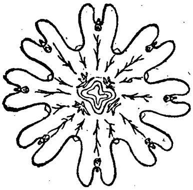


Strobila of Aurelia.

been mistaken forand described as an adult animal under that name.

After assuming this scyphistoma condition, transverse constrictions appear at regular intervals, dividing the column, as it were, into a pile of saucers; the edges rise, tentacles bud out, and the animal assumes the form seen in Fig. 65 (after Agassiz). The uppermost disk becomes detached, the rest separate one after the other and float away in the form of an "Ephyra" (Fig. 66, after A. Agassiz) and after some weeks assume the aurelia or adult condition (Fig. 67). The gigantic *Cyanea arctica*, which attains a diameter of from three to five feet across the disk, as Agassiz remarks, is produced from "a hydroid measuring not more than half an inch when full-grown."

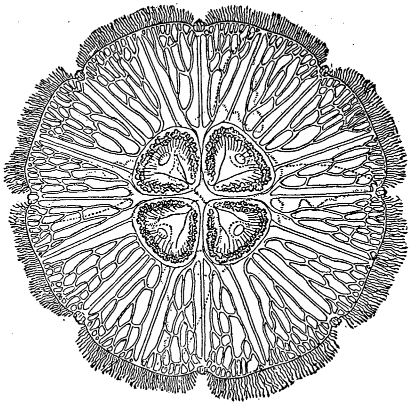
Fig. 66.



Ephyra of Aurelia.

On the other hand there are several exceptions known to this mode of development, a few growing directly from the egg, without passing through a hydra, or scyphistoma stage. Such is the large Pelagia, as observed by Krohn. Mr. A. Agassiz has observed the same fact in *Campanella pachyderma*, a minute jelly fish.

Fig. 67.



Aurelia flavidula. After Agassiz.

The Discophores, then, develop in two ways:—

A. Directly from the egg (Pelagia and Campanella).

B. From hydra-like young arising from eggs (Aurelia and Cyanea) and presenting the following phases of growth:—

1. Egg.
2. Morula (?)
3. Planula (Gastrula).
4. Scyphistoma.
5. Strobila.
6. Ephyra.
7. Aurelia (adult).

LITERATURE.

Nearly the same as for the Hydroids.

REVIEWS AND BOOK NOTICES.

Hayden's Geology of Colorado.[1]—Within this bulky volume of over seven hundred pages is contained a mass of geological, topographical and biological facts concerning Colorado, which it must be confessed reflect great credit on the management of the survey and the industry of the gentlemen employed upon it. Large appropriations have been made by the government for the survey, as accurate and timely information was wanted. We do not see but that ample and speedy returns have been made. The best possible topographical work was wanted, and the public have it from the best possible source. Information concerning the mines of Colorado is here given, while the bulk of the volume is taken up with the legitimate kind of work to be expected from such a survey. To this are to be added reports on the fossil animals and plants, and the living animals and plants of Colorado, thus making it a handbook for the general reader and traveller as well as scientist.

The geological and palæontological work (fossil plants as well as animals) and the living animals, are more fully illustrated than in former reports. The outline illustrations, showing the topography in combination with the geology, are admirable. We have

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[1] Annual Report of the United States Geological and Geographical Survey of the Territories, embracing Colorado, being a report of progress of the exploration for the year 1873. By F. V. Hayden, U. S. Geologist, Washington, D.C. 1874. 8vo. pp. 718. With maps and illustrations.